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Estimation Of Needle Populations

on Young, Open-Grown Douglas-Fir by Regression and Life Table Analysis

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[Pseudotsuga menziesii, life tables]

ABSTRACT

Needle populations of young, open-grown Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) can be estimated from regressions on tree height, stem diameter, crown width, number of limbs, number of branch tips, and foliated branch surface. A time-specific life table based on tree height and age appeared to realistically describe needle distributions by ages throughout the crown. The model also permitted evaluation of needle recruitment and loss for each tree age. In 13 years, the modeled tree recruited some 1.7 million needles and lost about 0.5 million needles to old age and the effects of extrinsic factors.

KEYWORDS: Douglas-fir, *Pseudotsuga menziesii*, foliage area.

CONTENTS

INTRODUCTION

Knowledge of a tree's leaf population and dynamics of leaf recruitment and loss is often needed for sampling pest populations and evaluating their impact on the host. To fill this need for young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), a foliage study was made in 1969 and 1970 on 40 seedling- and sapling-sized trees growing in 8 localities in Oregon and Washington.

The first objective of the study was to develop methods for estimating needle populations on whole trees and to relate that data to some of the common foliage units involved in sampling for insect populations. Papers consulted were those by Buchanan (1936), Kittredge (1944), and Whittaker and Woodwell (1968).

The second objective was to derive a realistic model for simulating annual needle recruitment, aging, and mortality on the whole tree. Madgwick (1968) proposed a crown model for red pine (*Pinus resinosa* Ait.) based on leader growth and amount of foliage in the topmost whorl. This paper presents a model in life table format.

The purpose of a life table is to simulate life history by recording populations from birth to death. The first life tables were employed by actuarial companies and later by entomologists and other animal biologists (Deevey 1947, Morris and Miller 1954, Harcourt 1969). Life tables have also been suggested for evaluating changes in plant numbers (Harcourt 1970, Waters 1969). The model most often used by entomologists is keyed to discrete generations in which a single cohort is followed through a specific aging period (age-specific life table). The model presented in this paper more closely resembles the one used by demographers and actuaries--that is, it deals with overlapping generations and is therefore keyed to specific time periods or anniversaries (time-specific life table).

METHODS AND PROCEDURES

Data were collected in mid-August and early September, after new growth had matured but before significant winter needle fall occurred. Study localities were near Randle (Woods Creek) in Washington and near Estacada (Fish Creek), Mill City (Green Basin), Upper Soda (Sheep Creek), Blue River (H. J. Andrews Experimental Forest), Tillamook (Kilchis River), Otis (Cascade Head Experimental Forest), and Corvallis (Mary's Peak) in Oregon. Median site index of the study areas was 116 (King 1966). Lowest site index was 106 at Estacada; highest was 142 at Tillamook.

Five open-grown, normal-appearing trees, ranging from 1.5 to 20 feet (0.46 to 6.1 m) tall were selected for foliage analysis at each locality. Each tree was cut and measured for height, age, stem diameter at ground level, width of crown at the widest point, and number of limbs. Starting at the bottom of the tree and working spirally up the stem, every fourth branch (nodal and internodal) was removed on trees taller than 2 feet (0.6 m) and measured for green weight, number of tips (fig. 1), and foliated area.[1] Every branch was taken on trees 2 feet (0.6 m) or less tall.

Foliage was clipped in the field from each branch and bagged according to whether the needles were from current

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[1] Foliated branch surface is the area of the branch occupied by foliage and originates from a sampling system devised by Morris (1955). It was determined by multiplying branch length by widest width and dividing by 2.

Figure 1.--Example of
3-year-old branch with
14 tips.

or older twigs and whether they came
from the upper or lower half of the crown.
Then, in the laboratory, the needles were
dried, removed from the branches,
weighed, and each bag proportionately
subsampled for determination of needle
populations in the various bags. These
numbers were then expanded to get the
total needle population for each tree.

The drying schedule for the foliage
was air-drying for about 30 days at room
temperature, then ovendrying for about
8 hours at 80° C. According to Forrest
(1968), this means respiration during the
prolonged air-drying period probably
reduced the final ovendry weights by at
least 8 percent. This was of no conse-
quence in this study because the interest
was needle numbers, not biomass. For
those interested, the ovendry weights
obtained are presented in appendix I.

Data were analyzed in a series of
regressions in which the independent
variables were:

X_1 -- Crown width, measured in feet.
X_2 -- Number of limbs on the tree,
both nodal and internodal
branches.
X_3 -- Foliated branch area, meas-

ured in square feet, (see
footnote 1).
X_4 -- Number of branch tips on the
tree or limb.
X_5 -- Tree height, measured in feet.
X_6 -- Tree age, determined by count-
ing rings at the severed base.
X_7 -- Stem diameter, measured in
inches at ground level.

Dependent variables were old and new
needles in one series of tests and number
of limbs, foliated branch area, and num-
ber of branch tips in another series. Be-
cause covariance tests with all the inde-
pendent variables revealed no significant
differences in regressions among plots,
the data from the eight study plots were
pooled and each tree treated as an inde-
pendent observation. A few trees were
dropped from some analyses because of
missing data for certain variables. Some
regression equations were presented in
log form (base 10) because of unequal
variances encountered between upper and
lower values of the independent variables.

RESULTS

FOLIAGE ESTIMATION ON
TREES AND LIMBS

Several tree measurements cor-
related well in single variable equations
with the number of needles on the tree
(table 1). As indicated by the coefficients
of determination (R^2), tree height, stem
diameter, crown width, branch tips, and
branch area accounted for about equal
amounts of variation in needle populations
on whole trees. Tree age with an R^2 of
0.62 gave a rather poor correlation,
probably because of difficulty in accurately
determining the true age of a tree. Fre-
quent false rings, apparently due to
numerous double flushes of growth in the
early years, seemed to be the cause for
the confusion.

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The E-value in table 1 is the antilog of the standard error of the estimate (S.E.E.) for the regression and is called the "estimate of relative error" by Whittaker and Woodwell (1968). An E of 1.30 means that an estimation of y (thousands of needles) from any single tree measurement (x) is expected to fall with the range of 1.30 y to y/1.30 (67 percent of the time). Thus, in table 1, the best estimators of needle populations, from the standpoint of least error, are the equations with the smallest E-values.

The large number of needles annually added to a tree was notable. As shown in the arithmetic plots in figure 2, new needles accounted for more than half the total needle population on trees up to a height of about 10 feet (3.0 m). On taller trees, the difference widened, but the number of new needles was still close to 50 percent of the total needle population. At first glance, this suggests that the needle population on 3- to 20-foot (0.9-to 6.1-m) trees about doubles each year. Actually, because of mortality in the older age class of needles, this is true

for only a couple of years of growth. Annual needle recruitment and mortality are presented in more detail in the section on modeling needle populations.

Multiple regressions, combining seven independent variables in all possible combinations (Grosenbaugh 1967), improved correlations with the number of needles on a tree, but not enough to warrant the trouble of taking several measurements. The best equation had five independent variables and an R^2 of 0.99.

Trees between 1 and 2 feet (0.30 to 0.61 m) tall had 44 percent or more of their total foliage in the upper half of the crown. But as the trees became older and growth rate increased, the ratio dropped sharply until trees 10 feet (3.05 m) tall and taller had little more than 7 percent of their foliage in the upper half of the crown (Log $Y = 0.7113 + 0.0146 \left(\frac{100}{X}\right)$; $r^2 = 0.48$). At least 70 percent of those needles were new. There was a slight but significant negative correlation between tree height and the percent

Table 1.--*Regression equations correlating old and new needles on seven independent variables associated with 1.5- to 20-foot (0.46- to 6.1-m) Douglas-firs (n = 35)*

| Variable		Regression equation (log base 10)	R^2	E
Y (thousands of needles)	X			
Total needles	Crown width	Log $Y = 0.8926 + 2.1101$ Log X_1	0.94	1.43
Total needles	Limbs	Log $Y = -2.3456 + 2.3532$ Log X_2	.84	1.78
Total needles	Branch area	Log $Y = 1.0165 + 0.4013$ Log $X_3 + .1591$ (Log X_3)^2	.97	1.40
Total needles	Branch tips	Log $Y = -0.7888 + 0.9834$ Log X_4	.98	1.23
Total needles	Height	Log $Y = 0.5011 + 1.9594$ Log X_5	.95	1.38
Total needles	Age	Log $Y = -1.1897 + 3.7695$ Log X_6	.62	2.47
Total needles	Stem diameter	Log $Y = 1.7513 + 1.8505$ Log X_7	.96	1.34
New needles	Height	Log $Y = .4069 + 1.7491$ Log X_5	.94	1.36
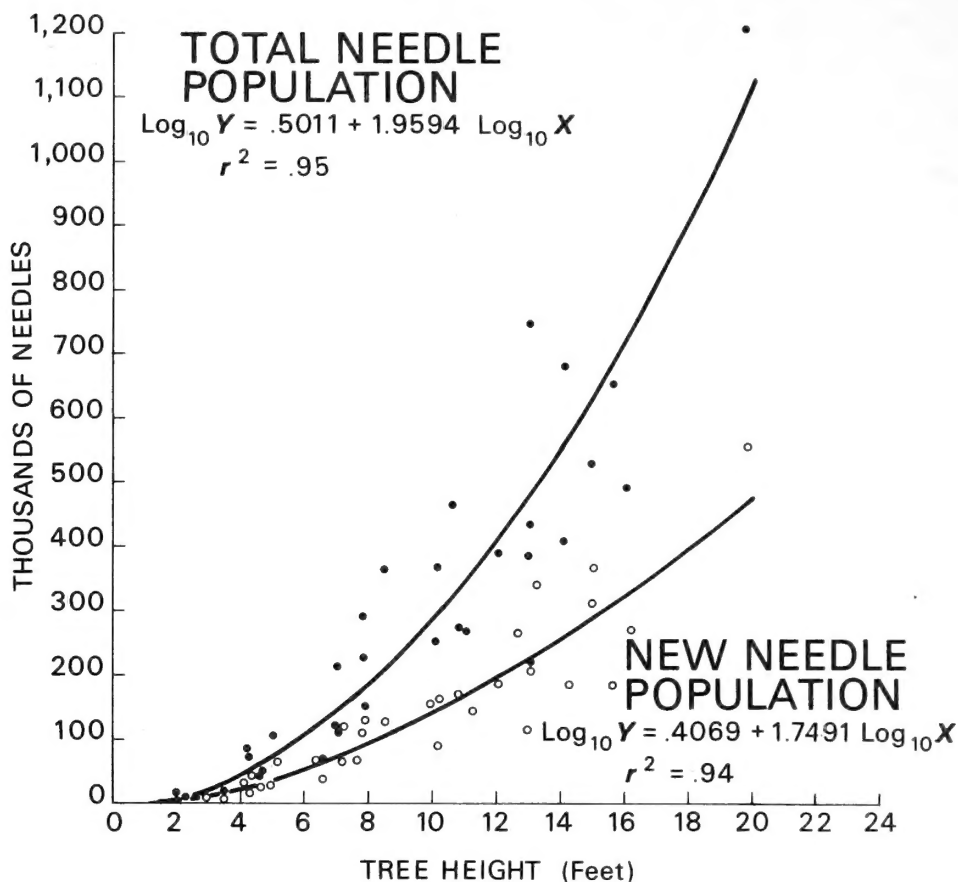
Figure 2.--Arithmetic plot of the log equations for total and new needle populations vs. tree height.

of new foliage in the upper crown ($Y = 93.94 - 0.73\ X$); however, variation was great ($r^2 = 0.136$).

Correlations of tree height and stem diameter with number of limbs, foliated branch area, and branch tips on the tree are shown in table 2. All correlations had good R^2 values, though number of limbs appeared to have more variability than number of branch tips or foliated branch area.

The e in table 2 has the same function as E in table 1. It is presented in lower case in table 2 because it is derived and applied somewhat differently

for arithmetic equations than for log equations. Here, an e is derived by dividing the S.E.E. by the mean value of y (Whittaker and Woodwell 1968). An e-value of 0.20 suggests that a single estimate of y will fall within ± 20 percent of the equation's estimate of y (67 percent of the time).

Needle populations on branches exposed to the sun were well correlated with measurements of foliated branch area, green weight of the whole limb, and the number of branch tips. Data are summarized as regression equations in table 3. Data were not collected for correlations on shaded branches.

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Table 2.--*Relationship between number of limbs, foliated branch area, and number of branch tips with tree height and stem diameter (n = 35)*

Dependent variable (Y)	Independent variable (X)	Regression equations	R^2	e
Number of limbs	Height	$Y = 25.171 + 7.864\ X$	0.79	0.22
Number of limbs	Stem diameter	$Y = 27.341 + 31.505\ X$	.80	.22
Foliated branch area	Height	$Y = -0.168 + 0.873\ X + 0.887\ X^2$	.89	.36
Foliated branch area	Stem diameter	$Y = -14.048 + 23.870\ X + 10.055\ X^2$	.94	.26
Number of branch tips	Height	$Y = -172.074 + 93.730\ X + 13.421\ X^2$	.91	.30
Number of branch tips	Stem diameter	$Y = -885.961 + 1364.092\ X$	.88	.34

Table 3.--*Relationship between number of needles on whole limbs and three easily measured independent variables (n = 80)*

Independent variable	Regression equations (log base 10)	R^2	E
Green branch weight (g)	$\text{Log } Y = 2.3122 + 0.7623 \text{ Log } X$	0.94	1.53
Foliated branch area (ft^2)[1]	$\text{Log } Y = 3.4924 + 0.9512 \text{ Log } X + 0.1820 (\text{Log } X)^2$	.91	1.48
Branch tips (number)	$\text{Log } Y = 2.5624 + 0.6027 \text{ Log } X + 0.0990 (\text{Log } X)^2$	.91	1.45

[1] Data apply only to branches exposed to the sun.

LIFE TABLE MODEL FOR EVALUATION OF NEEDLE DYNAMICS

Table 4 models the needle data of this study in life table form. Growth rate of the modeled tree (columns 1 and 2) is derived from the equation $\sqrt{\text{Height}} = 0.058 + 0.341 \text{ Age}$ (height in feet; age in years), the average growth rate of small Douglas-fir--up to 20 feet (6.1 m) tall--in stands rated site index 116.[2] Needle data in columns 3 and 4 were calculated from the two equations in figure 2.

[2] The growth equation curve was fitted to the restrictions stated by King (1966) that a tree from site index 116 should be about 4 feet (1.2 m) tall at age 6 and 20 feet (6.1 m) tall at age 13. A condition added by the author was that the tree should be 0.5 to 0.8 foot (0.15 - 0.24 m) tall at age 2. The equation for age in table 1 was rejected because of its low R^2 and because the tree's growth rate was not an accurate reflection of what was observed in the field.

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Table 4.--*Life table of needle populations on a Douglas-fir modeled to live 13 years on site index 116 with needles removed for senescence and loss due to extrinsic factors*

Tree age (years) (1)	Total height (feet) (2)	Total needle population (3)	Needle populations by age class					Needle loss		
			New (4)	1-year-old (5)	2-year-old (6)	3-year-old (7)	4-year-old (8)	Senescence (9)	Extrinsic factors (10)	Total (11)
1	0.16	1/ 87	87	--	--	--	--	0	0	0
2	.54	1/ 956	869	87	--	--	--	0	0	0
3	1.17	4,312	3,358	867	87	--	--	0	2	2
4	2.02	12,572	8,728	3,009	777	58	--	22	446	468
5	3.11	29,282	18,565	7,575	2,611	506	25	223	1,632	1,855
6	4.43	58,560	34,475	15,772	6,435	1,163	215	931	4,266	5,197
7	5.98	105,414	58,264	29,076	13,302	4,070	702	2,655	8,755	11,410
8	7.76	175,630	91,897	49,104	24,505	8,409	1,715	6,062	15,619	21,681
9	9.78	276,375	137,753	77,874	41,611	15,574	3,563	12,045	24,963	37,008
10	12.03	414,667	197,833	117,309	66,317	26,577	6,631	21,753	37,788	59,541
11	14.51	598,687	274,600	169,541	100,533	42,625	11,388	36,498	54,082	90,580
12	17.22	837,336	370,510	237,015	146,335	65,080	18,396	57,833	74,028	131,861
13	20.17	1,141,563	488,540	322,681	206,419	95,583	28,340	87,520	96,793	184,313
Totals			1,685,479					225,542	318,374	543,916

1/ Eight needles added to avoid negative needle fall.

Although complicated in appearance and derivation, the general principle of this type of life table is easy to grasp. After the number of needles the tree recruits each year is established, all needles are aged annually at the time of bud burst by moving them one column to the right and one row downwards. For example, in table 4, a 1-year-old tree starts out with 87 new needles. Next year, those 87 needles are 1-year-old and live on a tree that is 2 years old. At the same time, the tree recruits 869 new needles at bud burst, making a total of 956 needles on a 2-year-old tree. The next year, the original 87 needles become 2 years old, the 869 needles 1 year old, and the 3-year-old tree recruits 3,358 new needles. At this point, the table becomes complicated because some of the needles start to die. Appendix II accounts for mortality and how the completed schedule shown in table 4 is generated. It is sufficient here to say that some assumptions were made on when needles die of old age. The most obvious assumption from inspection of table 4

was that needles live no longer than 5 years. [3]

The fate of a cohort of needles recruited by a tree in any one year is seen by following them diagonally from left to right down the table. For example, the 3,358 needles recruited on the 3-year-old tree drops to 3,009 needles when the tree becomes 1 year older. In the next 3 years, the population of that cohort drops to 2,611 needles, 1,163 needles, and finally 702 needles the year before they all die.

The age-class distribution of needles on any tree of a particular age can be determined by reading along the horizontal. In table 5, needle distribution, expressed

[3] The author checked on needle mortality on all 40 plot trees as well as many other young Douglas-fir. Only rarely could trees be found with more than 5 years of needles on them. However, 7 years of needles were frequently observed on older trees (particularly on shaded branches), which agrees with the findings of Silver (1962).

as a percentage of the total needle population, shows that the proportion of needles in the various age classes changes greatly as the tree grows older. This partly reflects both the tree's declining capacity to increase needle production and also a constantly increasing reservoir of older needles being retained in the crown. Theoretically each tree will ultimately reach an age when needle production will about equal needle loss and the distribution of needles of different ages will stabilize.

As a partial check on the model, detailed foliage analyses were made of three young Douglas-firs growing on site index 116 land near Corvallis, Oregon. The age-class needle distribution on these trees (table 6) was rather close to that generated by the model in table 5.

Table 5.--*Distribution of Douglas-fir needles within each age class expressed as a percent of the total needle population on trees of that age (derived from table 4)*

Height (feet)	Tree age (years)	Total needle population	Distribution of needles in crown				
			New	1-year-old	2-year-old	3-year-old	4-year-old
		Number	- - - - - - - - - - - - *Percent* - - - - - - - - - - - -
0.16	1	87	100	--	--	--	--
.54	2	956[1/]	90.9	9.1	--	--	--
1.17	3	4,312	77.9	20.1	2.0	--	--
2.02	4	12,572	69.4	23.9	6.2	0.5	--
3.11	5	29,282	63.4	25.9	8.9	1.7	0.1
4.43	6	58,560	58.9	26.9	11.0	2.8	.4
5.98	7	105,414	55.3	27.6	12.6	3.9	.6
7.76	8	175,630	52.3	27.9	14.0	4.8	1.0
9.78	9	276,375	49.8	28.2	15.1	5.6	1.3
12.03	10	414,667	47.7	28.3	16.0	6.4	1.6
14.51	11	598,687	45.9	28.3	16.8	7.1	1.9
17.22	12	837,336	44.2	28.3	17.5	7.8	2.2
20.17	13	1,141,563	42.8	28.2	18.1	8.4	2.5

[1/] Eight needles added to avoid negative needle fall.

Table 6.--*Actual needle distribution on three Douglas-firs from site index 116 land near Corvallis, Oregon*

Height (feet)	Total needle population	Percent distribution of needles in crown				
		New	1-year-old	2-year-old	3-year-old	4-year-old
	Number	- - - - - - - - - - - *Percent* - - - - - - - - - - - -
6.0	83,140	51.5	24.7	19.0	4.5	0.3
9.8	318,809	50.6	25.3	19.0	4.7	.4
14.5	734,143	53.7	24.9	17.5	3.6	.3

Total needle production can be determined from table 4 for any given year up to age 13 by summing needle recruitment in column 4. For example, the model tree recruits 1,685,479 needles in its first 13 years, with about 68 percent of those needles still on the tree at the end of that period. Approximately 50 percent of all the needles recruited in 13 years stemmed from the last 2 years of growth-- 29 percent in the last year alone.

This appears to be a rapid increase, but in reality the tree is gradually slowing in its ability to recruit new needles. Table 7 shows how this pattern occurs. In this table, the number of tips on a tree is related to tree age (the first 3 years unreported since they extend beyond the field data). This relationship is examined because the reproductive capacity of tree foliage lies in the buds. Accordingly, an evaluation of tip production is a measure of the tree's capacity to increase needle numbers.

Annual tip production, the difference between any year's population and the population the year before ($N_t - N_{t-1}$), shows an impressive numerical increase in tips each year (table 7). What this reflects,

though, is the accumulative effects of prior tip multiplication. With Miller's (1965) technique of comparing tip production as a ratio of populations in adjacent years ($\frac{N_t}{N_{t-1}}$), it is found that the rate of increase per tip declines steadily as the tree grows older. It shows that a tree between the ages of 4 and 5 produces 3.46 new tips for each single tip the year before. Thereafter, the rate declines. By the 13th year, the reproductive rate is 1.33 tips per year. This ratio is essentially the same as the net reproduction-rate (r_0) described by Andrewartha and Birch (1954).

DISCUSSION

Most of the regression equations developed in this study accounted for a sizable amount of variation in estimating needle populations on young Douglas-fir and should be of value to field workers concerned with sampling and pest impact studies. For unknown reasons, the needle populations were much higher than those reported for Douglas-fir growing in Switzerland (Burger 1935). Perhaps the Swiss trees were competing with others. It is emphasized that the data

Table 7.--*Tip production as a measure of Douglas-fir's capacity to increase foliage*

Tree age (years)	Tree height (feet)	Total tips on trees (N)[1]	Annual tip recruitment $(N_t - N_{t-1})$	Tip recruitment ratio $\frac{N_t}{N_{t-1}}$
4	2.02	72	--	--
5	3.11	249	177	3.46
6	4.43	507	258	2.04
7	5.98	868	361	1.71
8	7.76	1,363	495	1.57
9	9.78	2,028	665	1.49
10	12.03	2,898	870	1.43
11	14.51	4,001	1,103	1.38
12	17.22	5,422	1,421	1.35
13	20.19	7,191	1,769	1.33

[1] From the equation $Y = -172.074 + 93.730 X + 13.421 X^2$ in table 2.

from this study apply only to open-grown trees. To estimate the number of needles per acre or per tree in situations where there is close competition among trees requires some evaluation of needle loss due to crowding.

It is also emphasized that the life table model presented in this paper is essentially a research hypothesis. Although the needle distribution generated compared favorably with three check trees, the mortality assumptions used to derive the distribution were based largely on observations rather than systematic study. Future research would require precise data on needle loss, with an accounting for the causes of needle mortality. For generalized conclusions and practicality in other research studies, the pertinent data should be obtained from trees on different sites and crown classes.

Basically, the life table format is a logical ledger in which to present needle data. Needles are recruited, age, and die just like other organisms for which life tables have been created. In fact, needle populations have unique characteristics which eliminate some of the more vexing problems associated with analyzing animal numbers by life tables. Needles have a distinct anniversary date, cohorts that can be followed rather closely, no problems with immigration and emigration, and no problems arising from changing sex ratios.

Most important, the analysis of needle life table data, in which the causes of mortality are identified and quantified, would provide much needed information on the relative importance of specific extrinsic factors, such as insects and diseases, as they relate to specific tree characteristics of growth, form, and appearance.

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APPENDIX I

Table 8.--*Mean ovendry weights of 100 new and old needles in the upper and lower crowns of short and tall trees*

Portion of tree	Tree height	Weight of 100 new needles		Weight of 100 old needles	
		Mean	S.D.	Mean	S.D.
	Feet	- - - - - - - - - *Grams* - - - - - - - -
Upper half of crown	1-10	0.387 ± 0.091		0.437 ± 0.111	
	10-20	.503 ± .077		.632 ± .135	
Lower half of crown	1-10	.263 ± .053		.350 ± .057	
	10-20	.355 ± .072		.457 ± .056	

Significant differences ($P < 0.01$) were noted in the weights between old and new needles, between needles from the upper and lower crown, and between needles on tall and short trees. No interaction effects were noted.

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APPENDIX II

The step-by-step details and assumptions involved in generating the life table shown in table 4 are as follows:

1. Establish growth rate for an average tree and record in columns 1 and 2. As described in the text, this was accomplished with the equation

$$\sqrt{\text{Height}} = 0.058 + 0.341 \text{ Age.}$$

2. Establish the total needle population for each tree height (equation in figure 2) and record in column 3.

3. Establish needle recruitment (new needle population) for each height of the tree (equation in figure 2) and record in column 4.

4. Establish needle mortality between anniversary dates (bud burst) by comparing the total needle population that could be on the tree with the actual population that exists. For example, the population on a 5-year-old tree could be all the needles that are on the tree at age 4 (12,572) plus the needles recruited at age 5 (18,565), making a total possible population of 31,137 needles. Since this is 1,855 more needles than the 29,282 needles actually existing on the 5-year-old tree, the difference must be needle mortality that occurred between the fourth and fifth anniversary dates. Needle loss is calculated in this way for each anniversary date and recorded in column 11.

5. Age the needles on each anniversary date and remove the needles that die. Starting with the first anniversary, the 87 needles recruited the first year are moved one column to the right and one row downwards. Thus, on the 2-year-old tree, there is a population of 869 newly recruited needles and 87 needles formed the year before. There is no mortality,

so no needles are removed. The next anniversary, the populations are again moved one column right and one row downward. But this year (3-year-old tree), 2 needles die (column 11) and must be removed to balance the population going into the third year. The removal of this mortality is recognition that needles die of old age or succumb to external factors of the environment, such as insects or disease. Accordingly, a death schedule must be established for senescence and mortality due to extrinsic factors. Working backwards, field observations showed that no needles survive to reach their fifth birthday. Also needle populations drop sharply between the third and fourth and second and third years. Less severe loss was observed in first- and second-year needles. Based on these observations, the following assumptions were established for removing dead needles: (a) new needles suffer no mortality; (b) senescence removes 25 percent of the needles aging from 2 to 3 years, 50 percent of the needles aging from 3 to 4 years, and all needles past the fourth year; (c) mortality not attributed to old age is designated as loss due to extrinsic factors and the needles are removed in proportion to the standing needle population in each age class.

6. Because the 3-year-old tree is not old enough to have needles die of old age, the two needles dying that year must be assigned to the impact of extrinsic factors (column 10). On a proportional basis, both are removed from the needle population reaching its first birthday, i.e., the 869 recruited on the 2-year-old tree becomes 867 needles on the 3-year-old tree. The next year, when the tree becomes 4 years old, 468 needles (column 11) must be removed. According to the assumptions on

senescence, the 87 needles passing from the second to the third year must lose 25 percent of its population (22 needles) due to old age. That leaves 446 needles (column 10) to be removed from the tree because of death by extrinsic factors. On a proportional basis, those 446 needles are removed thusly--349 needles from the population aging from new- to 1-year needles (3,358 - 349 = 3,009), 90 needles from the population aging from 1- to 2-year-old needles (867 - 90 = 777), and 7 needles from the population aging from 2- to 3-year-old needles (65 - 7 = 58), remembering that 22 needles were already removed from the original population of 87 needles for senescence. As in nature, the process is repeated year-by-year down the schedule until it is completed as in table 4. The important point to remember is that the mortality calculations require a form of double-entry accounting--mortality due to senescence is removed first; mortality from extrinsic factors removes what is left.

If the total impact of extrinsic factors on needle populations is needed, a theoretical schedule can be generated which removes only the needles dying of old age. Table 9 shows the result of such a simulation. It shows, instead of 225,542 needles dying of old age in 13 years (table 4), 351,796 needles would have died of senescence if they had lived their full life span. Thus the real impact of intrinsic factors is not the 318,314 needle loss shown in table 4, but rather the difference between the total mortality in table 4, less the mortality due to senescence in the theoretical table (543,916 - 351,796 = 192,120).

It is likely that the life table format is also suitable for studying other aspects of tree production, such as limbs or roots. Total limbs (or the like) could be determined by regression techniques for each age of the tree. Then, as in table 7, annual production for time t can be calculated by the formula $N_t - N_{t-1}$. Thus a matrix for distribution of limbs can be generated by age classes as in table 4. This, in turn, presents a research outline for determining survival rates at all stages of tree maturity.

Table 9.--*Theoretical life table for recruiting and aging of needles on young Douglas-fir, assuming the only mortality is due to senescence*

Tree age (years)	Tree height (feet)	Theoretical total needle population	New needle population (recruitment)	Theoretical needle distribution				Needle loss (senescence)
				1-year-old	2-year-old	3-year-old	4-year-old	
1	0.16	87	87	--	--	--	--	0
2	.54	956[1]/	869	87	--	--	--	0
3	1.17	4,314	3,358	869	87	--	--	0
4	2.02	13,020	8,728	3,358	869	65	--	22
5	3.11	31,336	18,565	8,728	3,358	652	33	249
6	4.43	64,613	34,475	18,565	8,728	2,519	326	1,198
7	5.98	119,110	58,264	34,475	18,565	6,546	1,260	3,767
8	7.76	201,833	91,897	58,264	34,475	13,924	3,273	9,174
9	9.78	320,732	137,753	91,897	58,264	25,856	6,962	18,854
10	12.03	484,109	197,833	137,753	91,897	43,698	12,928	34,456
11	14.51	700,958	274,600	197,833	137,753	68,923	21,849	57,751
12	17.22	980,720	370,510	274,600	197,833	103,315	34,462	90,748
13	20.17	1,333,683	488,540	370,510	274,600	148,375	51,658	135,577
Totals			1,685,479					351,796

[1]/ Eight needles added to avoid negative needle fall.

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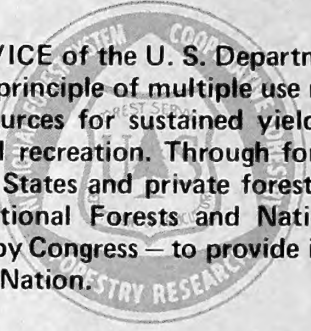
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